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安徽潜山古新世裂齿目一新属兼论中国古新世裂齿类[1)]

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摘要: 记述了安徽潜山盆地古新世裂齿目一新属种,命名为潜水本爱兽(*Benaius qianshuiensis* gen. et sp. nov.)。标本产于望虎墩组下段底部,为一带犬齿和完整颊齿列的左下颌骨。新种的主要特点是:个体较小,下齿列齿式2+?·1·4·3,i2略有增大,p1存在但退化成单根且侧扁,p3无下后尖,p4次臼齿化且无下内尖,下三角座前后压缩且下前尖退化,m3三叶。

中国曾经记述的和被认为是裂齿类的古新世哺乳动物共有9个属种:*Lofochaius brachyodus*、*Meiostylodon zaoshiensis*、*Anchilestes impolitus*、*Dysnoetodon minuta*、*Interogale datangensis*、*Plethorodon chienshanensis*、*Huananius youngi*、*Yuesthonyx tingae* 和 *Simplodon qianshanensis*。经过仔细比较研究它们的齿列,作者认为,*Lofochaius*、*Meiostylodon*、*Interogale*、*Plethorodon* 和 *Simplodon* 可能属于裂齿类,而 *Anchilestes*、*Dysnoetodon*、*Huananius* 和 *Yuesthonyx* 则可能与裂齿类没有很近的亲缘关系。广东南雄盆地上湖组 *Lofochaius brachyodus* 的P1和P2退化、P4有一定程度的臼齿化、外架窄、主尖锥状、前尖棱和后尖棱的颊侧端内收,显示了裂齿类的特点。湖南茶陵盆地枣市组 *Meiostylodon zaoshiensis* 的i2增大、上臼齿主尖锥状、柱尖和后附尖发育、前尖棱和后尖棱的颊侧端内收,与北美的 *Azygonyx* 和 *Esthonyx* 在形态上很相近,应该属于裂齿目。南雄盆地浓山组 *Interogale datangensis* 的下齿列中,i2增大、i3很小、p1缺失、下三角座前后压缩、m3具下次小尖叶等,都与裂齿类的特征相符。但它的一些特征,如釉质层覆盖i2整个冠面、p4的臼齿化程度低等,则可能代表了较原始的状态。潜山盆地望虎墩组下段 *Plethorodon chienshanensis* 的上臼齿外脊呈宽的U形、外架相对较窄、前尖和后尖锥形、柱尖和后附尖发育、无前附尖、前尖棱和后尖棱的颊侧端内收,这些特征都与典型的裂齿类相一致。潜山盆地望虎墩组上段 *Simplodon qianshanensis* 的前尖和后尖锥形、柱尖和后附尖发育、前齿带和后齿带显著等特点与裂齿类相似,但其前尖棱与柱尖不相连、原尖不膨大,则显示了它与已知裂齿类的区别,只能暂时归于裂齿目。

潜山盆地望虎墩组下段 *Anchilestes impolitus* 上臼齿的前尖和后尖锥形、外架较窄等与裂齿类相近,但其前尖棱和后尖棱的形态、下三角座和下跟座V形、m3没有下次小尖叶等明显地区别于已知的裂齿类,说明它可能不属于裂齿类。南雄盆地上湖组 *Dysnoetodon minuta* 的P4/4臼齿化程度很低、前尖棱和后尖棱的颊侧端外翻、下三角座和下跟座V形等特点与裂齿类明显不同,不应该归入裂齿类中。南雄盆地上湖组的 *Huananius youngi* 的一些特征,如下三角座和下跟座V形、柱尖和后附尖不发育、前尖棱和后尖棱的颊侧端外翻等特点说明它是一种钝脚类,而显著的单面高冠和与下后附尖相连的斜脊显示它很可能属于牧兽科(Pastoralodontidae)。另外,原作者将其归入裂齿类的特征并不是裂齿类所特有的。河南潭头盆地大章

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组 *Yuesthonyx tingae* 具有某些与裂齿类相似的特征,如 P1/1 退化、P4/4 次臼齿化、柱尖显著、m3 具下次小尖叶等。但它的犬齿大、外架宽、后附尖不发育、前尖棱和后尖棱的颊侧端外翻、上下颊齿的齿脊比较发育、下三角座前后向不压缩等特点,明显地区别于已知的裂齿类。

由于大多数原始裂齿类的标本不完整,缺失的信息很多,因而基于 25 个分类单元和 35 个齿列特征所做的系统发育分析,并没有对裂齿目中相关属级单元(特别是较原始类型)的系统关系给出很好的结果,但这个分析却对上述关于中国古新世属种归属的讨论提供了支持。

关键词: 中国安徽潜山,古新世,裂齿目

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A NEW PALEOCENE TILLODONT (TILLODONTIA, MAMMALIA) FROM QIANSHAN, ANHUI, WITH A REVIEW OF PALEOCENE TILLODONTS FROM CHINA

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Abstract A left lower jaw from the Paleocene Wanghudun Formation of the Qianshan Basin, Anhui Province, southern China is described. It represents a new genus and species of tillodont, named *Benaius qianshuiensis* gen. et sp. nov. The new species is characterized by the following features: size small, dental formula 2 + ? ·1 ·4 ·3, i2 not greatly enlarged, p1 present but reduced and laterally compressed, no metaconid on p3, and p4 submolarized without entoconid. Reexamination of dental features of the Chinese Paleocene tillodonts, including the originally assigned taxa and the reallocated forms of the order, suggests that *Lofochaius*, *Meiostylodon*, *Interogale*, *Plethorodon* and *Simplodon* have affinities to the order Tillodontia, whereas *Anchilestes*, *Dysnoetodon*, *Huananius*, and *Yuesthonyx* do not have close relationships to tillodonts. This conclusion is coincident with the result of the phylogenetic analysis on the basis of the dental characters.

Key words Qianshan, Anhui, China, Paleocene, Tillodontia

1 Introduction

The Tillodontia Marsh, 1875 is an extinct order of mammals whose fossils are known from the Paleogene in Holarctica. They lived in Asia and North America from the Paleocene to middle Eocene, while in Europe during the early and middle Eocene. The order was thought to have close relationships to arctocyonid condylarths (Gregory, 1910; Gazin, 1953; Van Valen, 1963; Rose, 1972; Szalay, 1977). McKenna (1975) classified the Tillodontia into the Mirorder Eparctocyona with Arctocyonia, Tubulidentata, Dinocerata, Embrithopoda, and Artiodactyla. Discoveries of early pantodonts and tillodonts made by the investigation of the "Red Beds" in southern China in 1970s led to the proposal of the hypothesis that tillodonts and pantodonts are closely related to each other (Chow and Wang, 1979), which was widely accepted (Gingerich and Gunnell, 1979; Lucas and Schoch, 1981; Stucky and Krishtalka, 1983; Lucas, 1993). McKenna and Bell (1997) further grouped the Tillodontia (as a suborder) with Didelphodonta, Apatotheria, Taeniodonta, Pantodonta, Pantolesta, Pholidota, and Ernanodonta in the order Cimolesta. However, this classification has not been widely followed (Miyata and Tomida, 1998a, b; Huang and Zheng, 1999, 2003; Tong et al., 2003). Since the phylogenetic relationships of the suborders of McKenna and Bell's (1997) Cimolesta remain unclear, Tillodontia is used as an ordinal group in this paper.

Tillodont fossils have been found in Holarctica. Five genera documented from North America are: *Esthonyx*, *Trogosus*, *Tillodon*, *Megalesthonyx*, and *Azygonyx* (Cope, 1874; Leidy, 1871; Gazin, 1953; Rose, 1972; Gingerich, 1989). Of them, *Azygonyx* is the only North American

Paleocene tillodont (Gingerich, 1989; Gingerich and Clyde, 2001). Two genera were reported from Europe: *Plesiesthonyx* and *Franchaius* (Lemoine, 1891; Baudry, 1992). Tillodonts from the Eocene of Asia include *Adapidium*, *Basalina*, *Kuanchuanius*, *Chungchienia*, *Higotherium*, and cf. *Trogosus* (Young, 1937; Dehm and Oettingen-Spielberg, 1958; Chow, 1963a, b; Lucas and Schoch, 1981; Cheng and Ma, 1990; Miyata and Tomida, 1998a, b). Tong and Wang (1998) noted the occurrence of a new tillodont in the Early Eocene Wutu Formation of Shandong Province without formal description. Asian Paleocene tillodonts were only collected in China. Paleocene fossils originally assigned to the order Tillodontia include six genera: *Lofochaius*, *Meiostylodon*, *Dysnoetodon*, *Huananius*, *Yuesthonyx*, and *Simplodon* (Chow et al., 1973; Wang, 1975; Zhang, 1980; Huang and Zheng, 1999, 2003; Tong et al., 2003). After their restudy of the type specimens of *Interogale* and *Anchilestes* from the Paleocene, Ting and Zheng (1989) referred these two genera to the order Tillodontia, in contrast to their previous allocation to Anagalida (Huang and Zheng, 1983; Qiu and Li, 1977). In addition, *Plethorodon*, originally considered to be a pantodont-like mammal (Huang and Zheng, 1987), was also reassigned to the order Tillodontia by some authors (de Muizon and Marshall, 1992; McKenna and Bell, 1997; Wang et al., 1998), while Tong et al. (2003) adhered to including it in the order Pantodonta.

Although the assignment of these tillodont or tillodont-like forms needs to be clarified, some of them may represent roots and/or stems of tillodonts. The record of the earliest and most primitive tillodonts in Asia indicates their Asian origin and dispersal from Asia to North America across Beringia during the late Paleocene and early Eocene (Krause and Maas, 1990; Beard, 1998a, b).

We report here a new tillodont from the Paleocene of the Qianshan Basin, Anhui Province, southern China. It is among the earliest records of the order Tillodontia in the world, and provides some new information to clarify the primitive features of this group. We follow Szalay (1969) and Zhou et al. (1975) in the use of descriptive terms for dental morphology.

During the study of the new material, comparison of crown structure with the primitive pattern of eutherian molars suggests the necessity in clarifying the terminology related to the description of the tillodont parastylar region. Currently, the nomenclatures widely used for describing molar structures were first proposed by Osborn (1907), and later revised and complemented by some researchers (Simpson, 1936; Van Valen, 1966; Szalay, 1969). In the description of tillodonts, many authors called the cusp or cuspidate structure at the anterolabial corner "parastyle", which connects paracone with paracrista (Rose, 1972; Gingerich and Gunnell, 1979; Stucky and Krishtalka, 1983; Baudry, 1992; Huang and Zheng, 1999, 2003; Tong et al., 2003). However, the cusp on the labial margin, connecting paracone with paracrista, was called "stylocone" in many papers with discussion of terminology, e.g. Van Valen (1966), Szalay (1969), and Zhou et al. (1975), while "parastyle" represents a cusp anterior to the stylocone, usually connecting the latter with a weak crest. The position of both stylocone and parastyle is clearly shown on the schematic diagrams (see Van Valen, 1966, fig. 1; Szalay, 1969, fig. 1 and Zhou et al., 1975, fig. 1). In this case, the "parastyle" described for tillodonts in previous papers is actually the stylocone. Calling that cusp "parastyle" may not be misunderstood in describing the tillodont fossils and making comparison within the group, but it does not correctly demonstrate the molar structure and creates confusion in comparison with other groups. In this paper, we use stylocone, instead of parastyle, to name the cusp that is at the anterolabial corner and connects paracone with paracrista.

2 Systematic paleontology

Order Tillodontia Marsh, 1875

Family incerte sedis

Benaius **gen. nov.**

Type species *Benaius qianshuiensis* gen. et sp. nov.

Diagnosis As that of the type and only species, *Benaius qianshuiensis* gen. et sp. nov.

Distribution So far known only from the Paleocene in China.

Etymology The genus is named after Mr. Ben'ai Yu, former director of the Administrative Office of Cultural Relics of Qianshan County, Anhui Province, for his support and assistance during our field work in Qianshan from the 1970s to 1990s.

Benaius qianshuiensis **gen. et sp. nov.**

(Fig. 1)

Holotype A left lower jaw with c～m3 (Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) catalogue number V 13806).

Locality and horizon The type and only specimen was collected from the Lower Member of the Wanghudun Formation at Fanglaowu, Wanghe Town, Qianshan County, Anhui Province. It is close to locality 71003 (Qiu et al., 1977) and both are at the lowest horizon yielding Paleocene mammals in the Qianshan Basin.

Diagnosis A small and primitive tillodont; dental formula 2 + ? ·1 ·4 ·3; i2 not greatly enlarged; p1 present but reduced and laterally compressed; no metaconid on p3; and p4 submolarized without entoconid.

Etymology The species name derives from the Qianshui River, one of two major rivers running through the Qianshan Basin, where the type specimen was collected.

Description The horizontal ramus of the lower jaw is fairly well-preserved, but the coronoid process, the angular process, and the condyle are damaged to different extents. The height of the horizontal ramus gradually increases posteriorly. On the lingual side of the lower jaw, a mandibular foramen is located on the ascending ramus, about the same level as the teeth. The distance from the foramen to the posterior end of the dentition is about 8.5 mm. The relatively weak symphysis is oblique, with its posterior end below the midpoint of p2. On the labial side, two mental foramina exist: one under p2 and the other beneath the point between p3 and p4.

The dental formula is 2 + ? ·1 ·4 ·3. None of the incisors are preserved, but two alveoli, for i2 and i3, are present. Damage at the anterior end of the lower jaw makes it impossible to be sure whether the animal has i1 or not, but the space between the symphysis and i2 alveolus suggests that i1 is probably smaller than the other two incisors, if it exists. According to the alveoli, both i2 and i3 are small, but i2 is slightly larger than i3, showing the tendency toward enlargement of i2. The crown of c1 was broken and its cross section is elliptic in outline. Posterior to the canine, a short diastema, 0.8 mm long, exists.

The cheek teeth of V 13806 are preserved in good condition. They increase in size from anterior to posterior (Table 1). The single-rooted first premolar (p1) is obviously reduced and laterally compressed. Its single main cusp is situated slightly anterior to the middle of the tooth. Two ridges extend forward and backward from the main cusp respectively, with two obscure cuspules at their ends. All the other cheek teeth are double-rooted. The p2 has also a single main cusp and its anterior cuspule (homologue of paraconid) is slightly larger. Instead of a cuspule at the end of the posterior ridge, it has a small heel with a cusp at its posterior end. The anterior cusp of p3 is positioned more lingually than that on p1 and p2, and looks more like a paraconid. An additional ridge runs down from the top of the protoconid on its lingual side. On the heel of p3, a ridge is anteroposteriorly aligned and a shelf-like structure is lingual to the ridge. The p4 is submolarized. It

Table 1 Measurements of the lower dentition of Benaius qianshuiensis **gen. et sp. nov.** (V 13806) (mm)

	c	p1	p2	p3	p4	m1	m2	m3	p1～p4	m1～m3	p1～m3
Length	2.14	2.08	3.02	3.61	4.32	4.48	4.98	6.61	13.00	15.97	28.96
Width (trd/tald)	1.72	1.20	1.55	2.30	3.12/2.30	3.84/3.84	4.31/3.88	3.79/3.27			

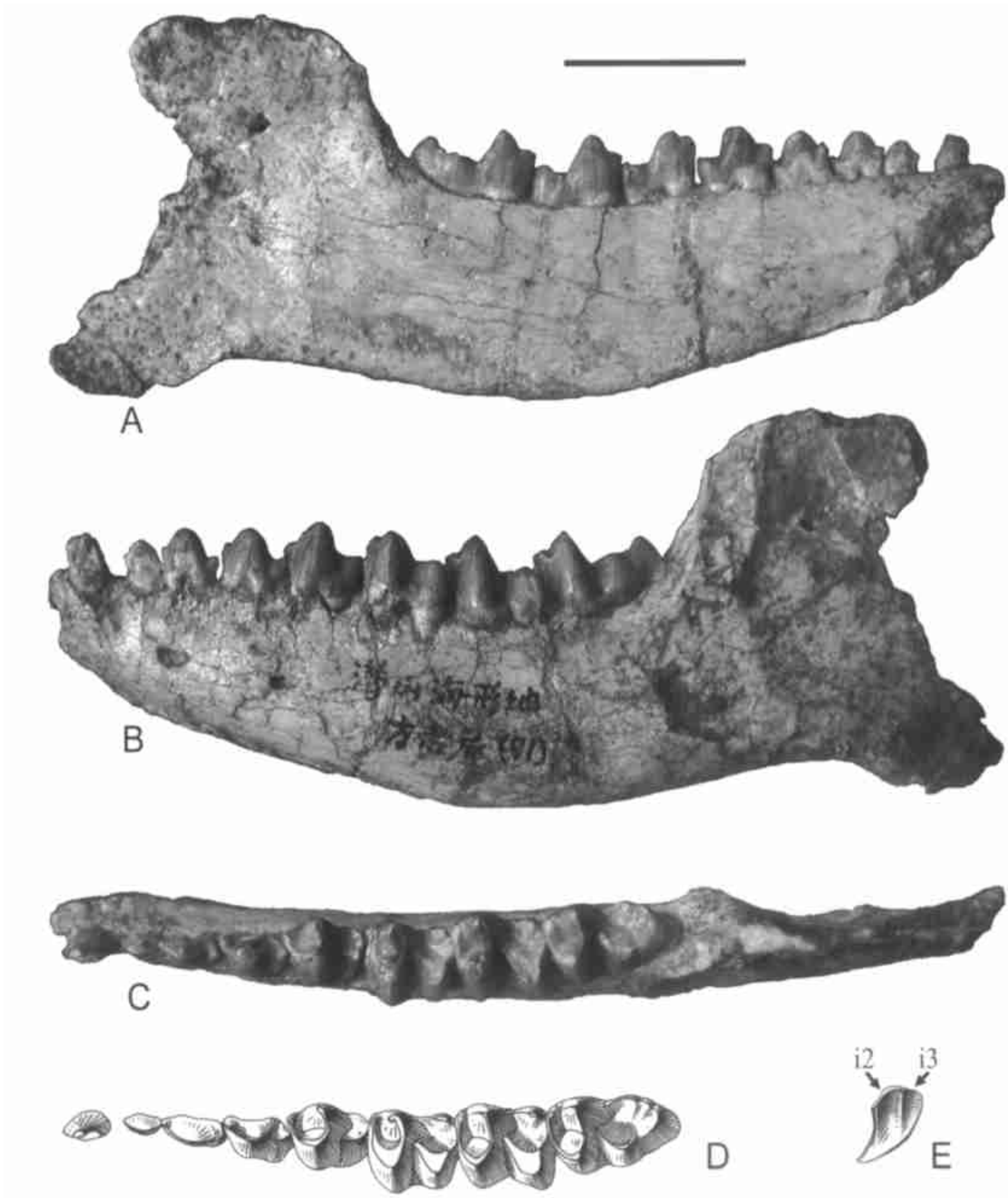


Fig. 1 Lower jaw of *Benaius qianshuiensis* gen. et sp. nov. (V 13806, holotype)
A. lingual view; B. labial view; C. crown view; D. line drawing of the dentition, crown view; E. anterior end of the jaw showing the alveoli for i2～i3, scale bar = 1 cm

has a fully developed trigonid and a talonid basin. Unlike on the molars, the paraconid of p4 is low and its trigonid opens wider. The talonid of p4 is relatively narrow without a distinct entoconid.

Trigonids of the molars are compressed anteroposteriorly to a certain extent. On the trigonid of each molar, the paraconid is reduced and metaconid is slightly higher than the protoconid. The talonid of m1 is morphologically identical to that of m2. The hypoconid is the largest cusp on the talonid. The hypoconulid is situated near the midline on the posterior margin. The entoconid is

distinct and separated from the hypoconulid by a small notch. The cristid obliqua originates from the point on the metacristid close to the metaconid. The talonid is as wide as the trigonid on m1, whereas it is narrower than the trigonid on m2. On the talonid of m3, the hypoconulid is enlarged and projects posteriorly, forming a third lobe.

Comparison and discussion The new specimen has a somewhat enlarged i2, a short diastema between canine and p1, a reduced p1, a submolarized p4, anteroposteriorly compressed trigonids on the lower molars with reduced paraconid, and a trilobed m3. The combination of these features suggests the similarity of the new specimen to the tillodonts. Thus, this animal is referred to the order Tillodontia.

Among the known tillodonts, the Eocene forms are usually much larger than the animal represented by the here described specimen. They have greatly enlarged I2/2 (some even rootless), no P1/1, distinct metastylids, and fused symphysis (when this feature is known). The new specimen is hence easily distinguished from the Eocene tillodonts.

Among the known Paleocene tillodonts, *Azygonyx* from the Clarkforkian of North America is the best documented genus. It differs from the Eocene *Esthonyx* only in having an unfused symphysis (Gingerich, 1989). Differences of V 13806 from the Eocene tillodonts can be used to distinguish it from *Azygonyx*, except the unfused symphysis. Chinese Paleocene mammals suggested to be tillodonts or tillodont-like forms include nine genera: *Lofochaius*, *Meiostylodon*, *Plethorodon*, *Interogale*, *Simplodon*, *Anchilestes*, *Dysnoetodon*, *Huananius*, and *Yuesthonyx*. Their affinities to the order Tillodontia are still in controversy. Of these forms, the first five are considered to be tillodonts in this paper, while the other four may not have tillodont affinities (see discussion below). *Lofochaius*, *Meiostylodon*, *Plethorodon*, and *Simplodon* are only represented by upper dentitions. Thus, the new specimen cannot be compared with them directly. *Plethorodon* and *Meiostylodon* are much larger than V 13806. In addition, the P1 of both *Plethorodon* and *Lofochaius* is double-rooted and not greatly reduced, which does not match V 13806. *Interogale* is represented by a pair of lower jaws. It is markedly smaller than V 13806 and has obviously enlarged i2 and no p1, which suggest that it represents a different genus from V 13806. *Anchilestes* has V-shaped trigonid and talonid, and less elongated m3 without hypoconulid, which are quite different from V 13806. *Dysnoetodon* is much smaller than the animal represented by the new specimen. Its p4 is not molarized, without a basined talonid, and both trigonid and talonid on molars are V-shaped. *Huananius* differs from the new specimen in having the following features: V-shaped trigonid and talonid, cristid obliqua extending to metastylid, better-developed crests on both trigonid and talonid. Moreover, *Huananius* is much larger in size. *Yuesthonyx* has relatively well-developed crests on both upper and lower cheek teeth, and less compressed trigonid and less reduced paraconid on molars. Its size is much larger than the new specimens as well.

In summary, the above discussion indicates that the new specimen probably represents a new genus and species of the order Tillodontia, here named *Benaius qianshuiensis* gen. et sp. nov. Because it has some features unknown in other tillodonts, its familial designation remains indeterminate.

3 Review of Chinese Paleocene tillodonts

Gazin (1953) noticed the similarities between Pantodonta and Tillodontia, but he suggested that the tillodonts differ from the pantodonts in having enlarged I2/2, no mesostyle, well developed hypocone shelf, anteroposteriorly compressed trigonid, and unilaterally hypsodont cheek teeth. With the discovery of more materials, however, some characters were found no longer available in distinguishing tillodonts from pantodonts, such as the development of mesostyle and hypocone shelf, and unilaterally hypsodont cheek teeth (Chow and Wang, 1979). When they suggested the affinity of *Anchilestes* and *Interogale* to tillodonts, Ting and Zheng (1989) pointed out that the

preprotocrista and postprotocrista, extending respectively to "parastyle" (= stylocone in this paper) and metastyle, and the well-developed hypocone shelf on tillodont upper molars are different from those of pantodonts, based on the comparison of *Anchilestes* and *Bemalambda*. Nevertheless, the affinity of *Anchilestes* to tillodonts has been questioned (Lucas, 1993; Wang et al., 1998), although Huang and Zheng (1999, 2003) and Tong et al. (2003) followed this assignment. Moreover, two such characters are not distinctive in certain forms of both orders. For example, the preprotocrista and postprotocrista of some pantodonts, e.g., pastoralodontids, pantolambdids, and barylambdids etc., extend respectively to stylocone and metastyle via paraconule and metaconule (Simons, 1960; Chow and Qi, 1978; Wang et al., 1992), as they do in tillodonts. Additionally, both pastoralodontids and alcidedorbinids have hypocone shelves on upper molars (Chow and Qi, 1978; de Muizon and Marshall, 1987, 1992; Wang et al., 1992).

Because of the similarities between tillodonts and pantodonts, it is not easy, in particular, to distinguish primitive tillodonts from primitive pantodonts. Apparently, the tillodonts have their own evolutionary pattern and represent a different lineage from the pantodonts at the ordinal (Gazin, 1953; Rose, 1972; Lucas, 1993; Ting and Zheng, 1989; Tong et al., 2003) or subordinal level (Chow and Wang, 1979; Van Valen, 1963; McKenna and Bell, 1997). For instance, the development of rodent-like chisel incisors from the I2/2 enlargement in tillodonts is definitely distinct from the unchanged incisor pattern thoroughout pantodont history. Some other dental characters may also demonstrate the differentiation between tillodonts and pantodonts (Table 2). Differences of certain characters seem to be minor, but their stable appearance in unambiguous members of both groups indicates that such differences are not superficial and may be diagnostic of the order Tillodontia.

Table 2 Comparison of some dental characters of Tillodontia and Pantodonta

characters	Tillodontia	Pantodonta
1. incisors	I2/2 enlarged, rooted or rootless	increased posteriorly or subequal in size
2. paracone and metacone	conical in general	labial wall flattening or crescentic
3. last upper and lower premolars	somehow molarized	less molarized
4. width of stylar shelf	moderately wide, narrower with respect to that of pantodonts	wide, near or more than half width of the tooth
5. stylocone	well developed	not well defined
6. parastyle	absent	vestigial, having weak crest connecting stylocone
7. metastyle	well developed	vestigial or absent
8. paracrista and metacrista	adducted at their labial ends	abducted at their labial ends
9. trigonid	anteroposteriorly compressed and U-shaped	not compressed and V-shaped
10. talonid	usually U-shaped	V-shaped
11. talonid of m3	with hypoconulid lobe (bilobed)	without hypoconulid lobe

As mentioned above, nine genera and species from the Paleocene of China have been reported or suspected to be tillodonts. The systematic position of some of them remains controversial (Zhang, 1980; Huang and Zheng, 1987, 1999, 2003; Ting and Zheng, 1989; Baudry, 1992; de Muizon and Marshall, 1992; Lucas, 1993; Wang et al., 1998; Tong et al., 2003).

Lofochaius brachyodus Chow et al., 1973, from the Shanghu Formation of the Nanxiong Basin, Guangdong Province, is the first named Chinese Paleocene tillodont. It was described in detail by Zhou et al. (1977). Ting and Zheng (1989) considered that it was different from other tillodonts in terms of preprotocrista and postprotocrista extending respectively to paracone and

metacone. Although this opinion was followed by Huang and Zheng (1999, 2003), *Lofochaius* was referred to the order Tillodontia by most authors (Baudry, 1992; Lucas, 1993; Wang et al., 1998; Ting, 1998; Lucas and Schoch, 1998). Tong et al. (2003) listed some dental characters of *Lofochaius*, e.g., reduced P1 and P2, P4 somewhat molarized, narrow stylar shelf, and conical main cusps, and considered it likely to be a tillodont. In addition, preprotocrista and postprotocrista of *Lofochaius*, extending respectively to paracone and metacone (emphasized by Ting and Zheng, 1989), may indicate a primitive state related to the less-developed conules. *Lofochaius* probably represents a primitive tillodont.

Specimens of *Meiostylodon zaoshiensis* Wang, 1975, were collected from the Zaoshi Formation of the Chaling Basin, Hunan Province. The morphological features of its upper molars are close to those of *Esthonyx* from North America (Wang, 1975). Its placement in the order Tillodontia has not been challenged (Lucas, 1993; Wang et al., 1998; Huang and Zheng, 1999, 2003; Tong et al., 2003). Its conical main cusps, stylar shelf at one-third width of the molar, well-developed stylocone and metastyle, and labially adducted paracrista and metacrista suggest a tillodont affinity.

Anchilestes impolitus Qiu and Li, 1977, from the Lower Member of the Wanghudun Formation of the Qianshan Basin, Anhui Province, was originally assigned to Zalambdalestidae. Ting and Zheng (1989) referred it to the order Tillodontia. This assignment was questioned later (Lucas, 1993; Wang et al., 1998), but it was followed in some publications, e.g., Baudry (1992), McKenna and Bell (1997), Huang and Zheng (1999, 2003), and Tong et al. (2003). In fact, *Anchilestes* has some similarities to tillodonts, which include conical paracone and metacone, and relatively narrow stylar shelf. On the other hand, the pattern of its paracrista and metacrista, V-shaped trigonid and talonid, and no hypoconulid lobe on m3 are distinctive from the known tillodonts. *Anchilestes* is excluded from the order Tillodontia in this paper. The resolution of its systematic position awaits discovery of better and more complete specimens.

Dysnoetodon minuta Zhang, 1980, is from the Shanghu Formation of the Nanxiong Basin, Guangdong Province. It was first thought to be a tillodont-like mammal, but the original author also noticed its differences from tillodonts. The poor preservation of the specimens hampered further discussion of its phylogenetic relationships, but the clear differences led to its exclusion from the order Tillodontia (Huang and Zheng, 1999, 2003; Tong et al., 2003). Additionally, Ting and Zheng (1989) first emphasized the similarities of its paratype specimen (V 5838) to the South American pantodont *Alcidedorbinya*. McKenna and Bell (1997) further grouped *Dysnoetodon* and *Harpyodus* in the family Harpyodidae of Pantodonta without any discussion. Whether it is a pantodont or not, *Dysnoetodon* is unlikely to be a Paleocene representative of tillodonts.

Interogale datangensis Huang and Zheng, 1983, was collected from the Nongshan Formation of the Nanxiong Basin, Guangdong Province, and originally referred to Anagalida with family undetermined. Ting and Zheng (1989) restudied the type specimen and assigned it to the order Tillodontia. While questioned by Lucas (1993), this assignment was widely accepted (Baudry, 1992; McKenna and Bell, 1997; Wang et al., 1998; Ting, 1998; Huang and Zheng, 1999, 2003; Tong et al., 2003). The lower dentition of *Interogale* has enlarged i2 (though not as distinct as *Esthonyx*), very small i3, no p1, anteroposteriorly compressed trigonid, and hypoconulid lobe on m3, which is strongly indicative of its affinity to tillodonts. Its remarkable differences from the most primitive North American tillodont, *Azygonyx*, i.e., i2 crown completely covered with enamel and less molarized p3～4, should represent a more primitive state than *Azygonyx*, as Ting and Zheng (1989) stated. The lack of p1 may suggest it is somewhat derived in this aspect.

Plethorodon chienshanensis Huang and Zheng, 1987, is from the Lower Member of the Wanghudun Formation in the Qianshan Basin, Anhui Province and tentatively assigned to the order Pantodonta. Later, de Muizon and Marshall (1992) considered it to be a tillodont instead of a pantodont. This opinion was followed by McKenna and Bell (1997) and Wang et al. (1998), but disputed by Ting (1998) and Tong et al. (2003). Upper molars of *Plethorodon* have wide U-

shaped ectolophs, relatively narrow stylar shelf, conical paracone and metacone, well-developed stylocone and metastyle, no parastyle. Its paracrista and metacrista adducted labially. These features have also been found in some typical tillodonts and accord with the diagnostic characters discussed above.

Huananius youngi Huang and Zheng, 1999, is represented by fragmentary right upper and lower jaws of the same individual from the Shanghu Formation of the Nanxiong Basin, Guangdong Province. The original authors referred it to the order Tillodontia, based on the presence of unilaterally hypsodont cheek teeth, well-developed pre- and postcingulum, weak hypocone shelf, distinct conules, a small rounded talonid on p4, nearly equal-sized trigonid and talonid on m1～2, and pronounced metastylid (Huang and Zheng, 1999). Tong et al. (2003) further mentioned that *Huananius* has paracrista and metacrista extending respectively to "parastyle" (= stylocone in this paper) and metastyle, and V-shaped trigonid and talonid, and thought these characters to be indicative of tillodont affinity. However, none of these characters nor their combination is exclusively indicative of tillodonts. In fact, the characters, such as V-shaped trigonid and talonid, cristid obliqua extending to metastylid, undeveloped stylocone and metastyle, and both paracrista and metacrista abducted at their labial ends, show that *Huananius* is a pantodont, probably a pastoralodontid.

Yuesthonyx tingae Tong et al., 2003, is from the Dazhang Formation of the Tantou Basin, Henan Province. It was originally referred to the order Tillodontia, but the original authors (Tong et al., 2003) noticed that it has some morphological features different from other known tillodonts. The specimens of *Yuesthonyx* have some characters close to tillodonts on the one hand, which include reduced P1/1, diastema at the anterior part of the dentition, submolarized P4/4 with an incipient metacone on the upper and a talonid basin on the lower, distinct stylocone on upper molars, and m3 with the hypoconulid lobe. On the other hand, some features show its similarities to pantodonts: large canines, relatively wide stylar shelf, undeveloped metastyle, paracrista and metacrista abducted at their labial ends, relatively well-developed cristae on both upper and lower cheek teeth, and less compressed trigonids. The combination of dental features of *Yuesthonyx* may not suggest its affinity to tillodonts with any certainty.

Simplodon qianshanensis Huang and Zheng, 2003, is the most recently named tillodont, and was collected from the Upper Member of the Wanghudun Formation in the Qianshan Basin, Anhui Province. The upper molars of *Simplodon* have conical paracone and metacone, well-developed stylocone and metastyle, relatively narrow stylar shelf, and distinct precingulum and postcingulum. These characters show that *Simplodon* is similar to tillodonts. At the same time, *Simplodon* differs from other tillodonts in having paracrista disconnected from the stylocone, and less swollen protocone. We, therefore, follow Huang and Zheng (2003) in considering *Simplodon* a tillodont-like mammal and assigning it tentatively to the order Tillodontia.

4　Remarks on phylogenetic relationships within Tillodontia

Phylogenetic relationships among tillodont genera were discussed by some researchers, but no phylogenetic analysis has yet been conducted. Relationships were only inferred or hypothesized due to the fragmentary material of most taxa (Rose, 1972; Stucky and Krishtalka, 1983; Gingerich, 1989; Baudry, 1992; Lucas, 1993; Chow et al., 1996; Miyata and Tomida, 1998a). In this paper, we attempt to carry out an analysis using the cladistic method.

Pantodonts are currently thought to be closely related to tillodonts (Chow and Wang, 1979; Gingerich and Gunnell, 1979; Lucas and Schoch, 1981; Stucky and Krishtalka, 1983; Lucas, 1993; Huang and Zheng, 1999, 2003; Tong et al., 2003), so some pantodont genera were chosen for the analysis, including *Alcidedorbinya*, *Altilambda*, *Pantolambda*, and *Archaeolambda*. *Deltatherium* was also included, because Lucas (1993) used it as an outgroup to hypothesize the

phylogeny of tillodonts. Like other mammalian lineages, parallelism of character transformation also existed in tillodonts compared with other groups, as noted by Gazin (1953) and Lucas (1993). An outgroup is hypothesized in helping determine the polarization of character states on the basis of wide comparison with primitive eutherians. We are willing to analyze all tillodont genera, but three poorly documented genera, *Basalina*, *Chungchienia*, and *Higotherium*, are excluded from the analysis. As mentioned above, some taxa were tentatively referred to the order Tillodontia and their systematic position is in debate. Inclusion of these taxa is to evaluate their relationships to the true tillodonts.

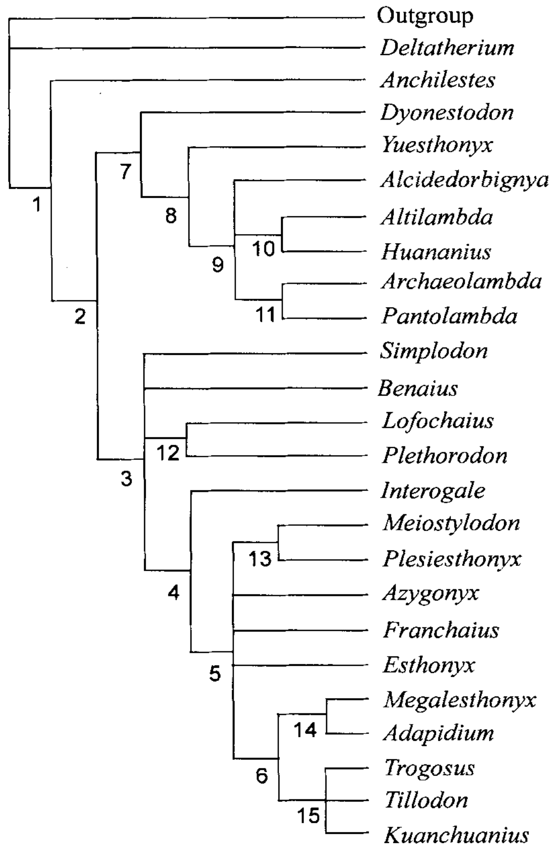


Fig. 2 Strict consensus tree showing the possible phylogenetic relationships of tillodonts and other selected mammals

Since most tillodont taxa are represented by upper and/or lower jaws, the analysis only deals with dental characters. The dataset comprises 35 dental characters of 25 taxa (see Appendix I and II). Using the heuristic algorithms search (Swofford, 2000), PAUP generated 90 most parsimonious trees (tree length = 102, CI = 0.5000, RI = 0.7475, RC = 0.3738). This is probably due to the incomplete materials known for many tillodont forms. The strict consensus tree (Fig. 2) provides a primary framework for understanding the phylogenetic relationships of tillodonts. According to the consensus tree, a monophyletic group (node 3), including *Simplodon*, *Benaius*, *Lofochaius*, *Plethorodon*, *Interogale*, *Meiostylodon*, *Plesiesthonyx*, *Azygonyx*, *Franchaius*, *Esthonyx*, *Megalesthonyx*, *Adapidium*, *Trogosus*, *Tillodon*, and *Kuanchuanius*, is supported by the analysis. They are referred to the order Tillodontia in this paper. The analysis also supports another monophyletic group (node 4), consisting of *Interogale*, *Meiostylodon*, *Plesiesthonyx*, *Azygonyx*, *Franchaius*, *Esthonyx*, *Megalesthonyx*, *Adapidium*, *Trogosus*, *Tillodon*, and *Kuanchuanius*. In this group, *Interogale* forms the sistergroup to that including the remainders (node 5). In addition, three most derived tillodont taxa in the analysis, *Trogosus*, *Tillodon*, and *Kuanchuanius*, form a monophyletic group (node 15), while *Megalesthonyx* and *Adapidium* form another one (node 14) that is sistergroup of the *Trogosus*-*Tillodon*-*Kuanchuanius* group.

Because most primitive tillodonts are not well-documented and many dental characters are missing in these taxa, the analysis failed to clarify their phylogenetic relationships within the order Tillodontia. Discovery of more complete and better-preserved specimens of these taxa will considerably help in solving this problem.

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Appendix I Characters used for phylogenetic analysis within Tillodontia. An asterisk (*) indicates an ordered multistate character.

1. Upper incisor number : (0) three ; (1) less than three.
2. Lower incisor number : (0) three ; (1) less than three.
3. Relative size of incisors : (0) none obviously enlarged ; (1) I2/2 enlarged ; (2) I2/2 strongly enlarged ; (3) I2/2 rootless. *
4. I2 and i2 enemal : (0) covering whole crown ; (1) restricted to anterior side.
5. P1/1 : (0) present ; (1) absent.
6. P1/1 root : (0) two ; (1) less than two.
7. P2 : (0) two roots ; (1) single root ; (2) tree roots.
8. P3～4 : (0) not double V-shaped ; (1) double V-shaped.
9. P3～4/3～4 : (0) submolarized ; (1) highly molarized.
10. Upper molars : (0) strongly transversely elongated ; (1) moderately transversely elongated ; (2) subequal in length and width. *
11. Protocone of upper molars : (0) anteroposteriorly short ; (1) anteroposteriorly long.
12. Width of stylar shelf : (0) narrow ; (1) wide but less than half width of the molar ; (2) wide and equal to or more than half width of the molar.
13. Extoflexus : (0) deep ; (1) shallow.
14. Centrocrista : (0) undeveloped ; (1) developed.
15. Main cusps of upper molars : (0) conical ; (1) labial wall flattening ; (2) crescentic. *
16. Paracrista and metacrista : (0) undeveloped ; (1) developed.
17. Paracrista and metacrista : (0) neither abducted nor adducted labially ; (1) adducted labially ; (2) abducted labially.
18. Parastyle : (0) developed ; (1) vestigial ; (2) absent. *
19. Mesostyle : (0) no ; (1) small ; (2) large. *
20. Metastyle : (0) developed ; (1) undeveloped ; (2) absent.
21. Stylocone : (0) developed ; (1) undeveloped.
22. Ectocingulum : (0) low ; (1) well developed.
23. Postcingulum : (0) undeveloped ; (1) well developed ; (2) forming hypocone shelf. *
24. Unilateral hypsodonty : (0) unclear ; (1) distinct ; (2) very strong ; (3) only labial side covered with enemal and rootless.
25. p2 : (0) two roots ; (1) single root.
26. Metaconid of lower molars : (0) apparently smaller than protoconid ; (1) subequal to protoconid ; (2) apparently larger than

protoconid.

27. Position of hypoconulid: (0) close to labial side, talonid not V-shaped; (1) close to lingual side, talonid V-shaped.

28. Cristid obliqua: (0) at midline or labially; (1) between midline to metaconid; (2) metastylid.

29. Entoconid: (0) developed; (1) undeveloped; (2) absent.

30. Metastylid: (0) absent; (1) present.

31. Height difference between trigonid and talonid: (0) large; (1) small.

32. Lower molar trigonid: (0) anteroposteriorly compressed; (1) open.

33. Trigonid shape of lower molars: (0) U-shaped; (1) V-shaped.

34. m3 talonid elongation: (0) not elongated; (1) apparently elongated; (2) forming hypoconulid lobe. *

35. Lower jaw symphysis: (0) unfused; (1) fused.

Appendix II Data matrix showing the distribution of 35 characters among 25 taxa that were analyzed using the heuristic algorithms of PAUP. Characters scored "0" represents the ancestral state or primitive state, and characters scored "1" through "3" represent derived states. The "A" refers to the score "0 + 1". The "?" denotes missing data.

	1 1234567890	1111111112 1234567890	2222222223 1234567890	33333 12345
Outgroup	0000000000	0000000000	0000000000	00000
Deltatherium	0000110001	0010000100	0000010020	0111?
Alcidedorbignya	0000011101	1001112101	1011111101	11110
Altilambda	0000010101	1211112121	1122011211	11110
Huananius	???????101	120101211?	1122?11211	011??
Archaeolambda	0000002102	1201212112	1000011121	11110
Pantolambda	0000012101	1201212111	1010011120	11110
Dyonestodon	????0100?1	1201012101	1020011010	1112?
Yuesthonyx	??0?012011	1111112121	0110011100	01120
Lofochaius	????000001	1011011200	002???????	?????
Plethorodon	????000001	1011011200	002???????	?????
Meiostylodon	??1??????0	1011011200	012???????	?????
Simplodon	???????001	0011011100	002???????	?????
Azygonyx	1021110011	1010001200	0021010001	10020
Esthonyx	1021111011	1011011200	0021010001	10021
Trogosus	1031111011	1111011200	0022110101	11021
Tillodon	1131111011	1111011200	0022110101	11021
Anchilestes	???????000	0100012101	0120?101?0	0011?
Adapidium	???????012	1111011220	112??21101	1002?
Megalesthonyx	?02111?011	1111011220	1122010101	10021
Franchaius	???????01A	10A1011200	0021?10001	100??
Plesiesthonyx	?????????1	1011011200	0121?10011	1002?
Kuanchuanius	?03111?01?	?????112?0	0022110101	11021
Interogale	?01011??0?	??????????	???0010000	10020
Benaius	?01?01??0?	??????????	???0010100	10020